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THE SYSTEMATICS AND ECOLOGY OF POISON-IVY AND THE POISON-OAKS (TOXICODENDRON, ANACARDIACEAE)[1]

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(Continued from page 443)

ECOLOGICAL LIFE HISTORY

The bulk of scattered information about the natural history of *Toxicodendron* sect. *Toxicodendron* is here summarized as an ecological life history. The pattern followed is essentially a synthesis of the pattern of the Biological Flora of the British Isles format as published in the Journal of Ecology and the outline suggested by Pelton (1951). Inasmuch as most of the material relating to anatomy, morphology, hybridization, and taxonomy is included elsewhere, such material is not repeated; only additional topics will be discussed. Excluded from discussion is sect. *Simplicifolia* which includes only *T. borneense* about which virtually no data are available.

MORPHOLOGICAL LIMITS

Although the total length of time to elapse from the time of seed germination until the time a young plant can produce flowers is not known for all taxa, plantation studies of *Toxicodendron radicans* subsp. *negundo* have shown that three years were required for plants to progress from seed to flowering stage. The longevity of the species is unknown. However, trunks of *T. radicans* subsp. *negundo* are known

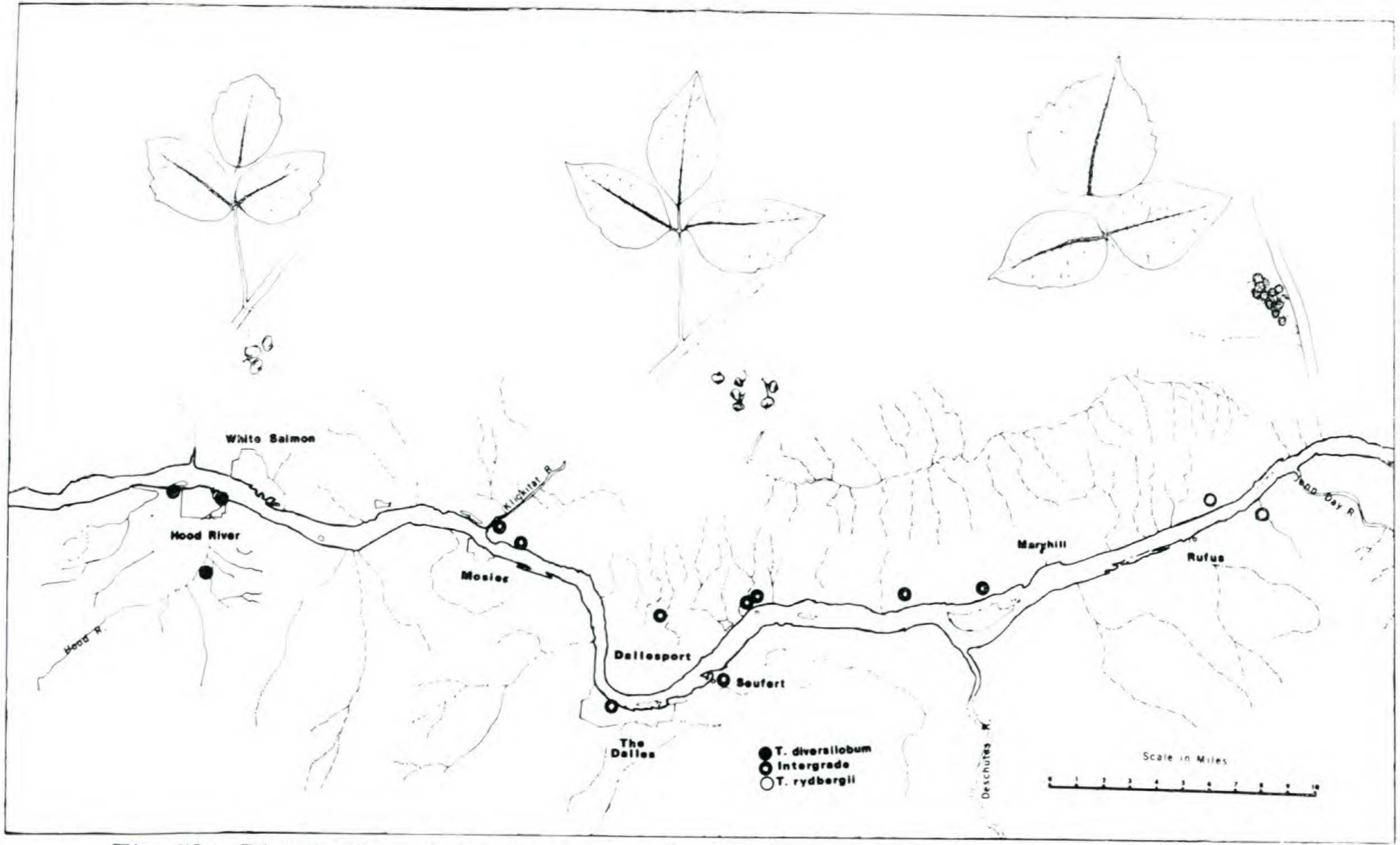

Fig. 53. Distribution of *Toxicodendron diversilobum* and *T. rydbergii* in the Columbia River gorge of Oregon and Washington and location of intergrades between them. (See text, page 423).

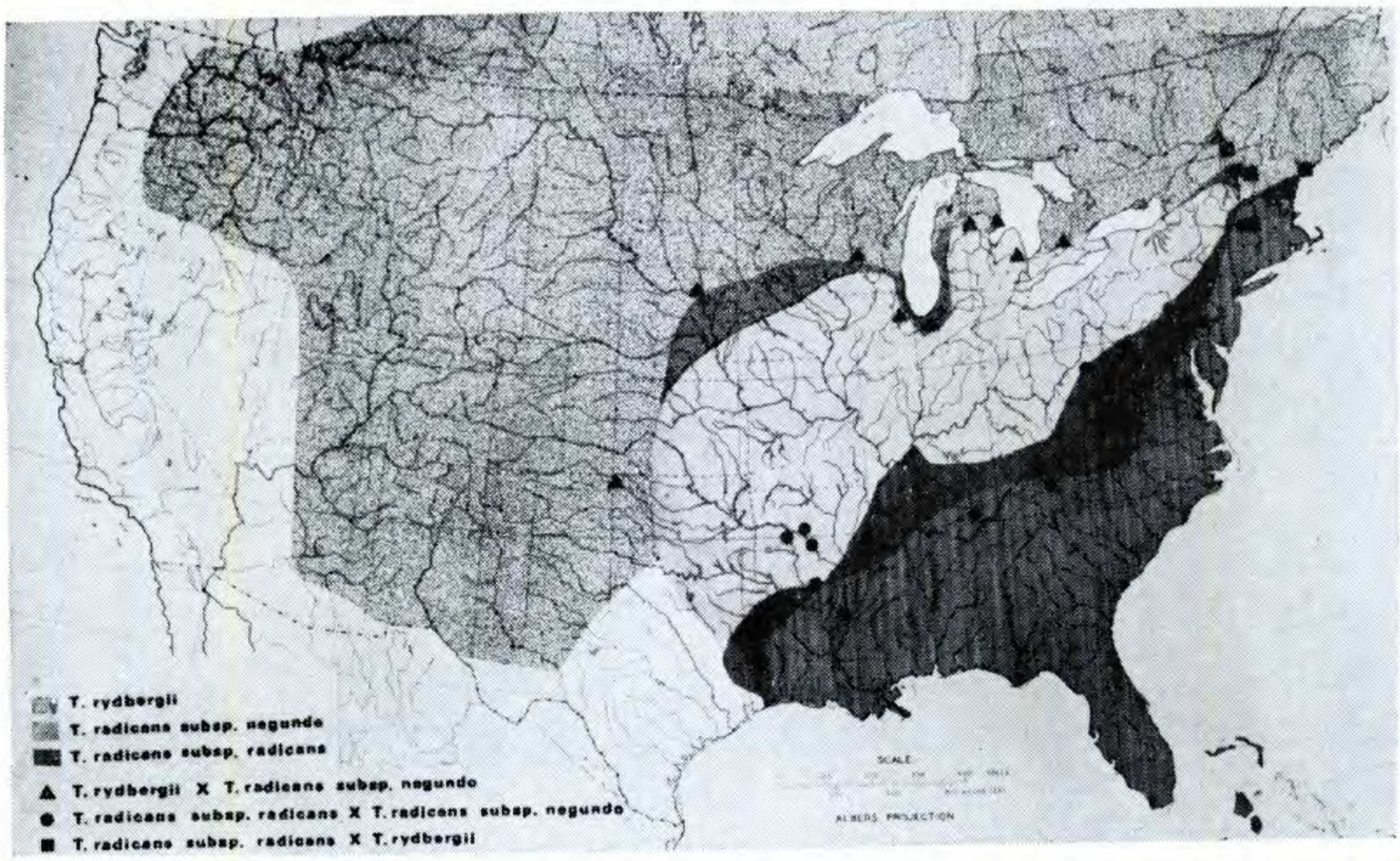

Fig. 54. Distribution of 3 taxa of poison-ivy in the United States and Canada and location of intergrades between them. (See text, page 436).

Fig. 55. Distribution of 2 taxa of poison-ivy in Mexico and location of intergrades between them. (See text, page 423).

up to 12 cm across, bearing 38 growth rings. The widely distributed collection of George Cooley (No. 2499) of *T. radicans* subsp. *radicans* from Sanibel Island, Florida, represents a tree of some five meters in height. This same individual tree is reported to have had a trunk diameter of 9 cm dbh, with one of its branches 13 dm long bearing 6130 flowers! (Cooley, 1955) Trunks of even larger *T. diversilobum* individuals have been reported in California.

ALTITUDINAL LIMITS

Data on elevation extremes for each species and subspecies are summarized in Table 15. The data come primarily from herbarium information. They are only approximate. Except for relatively high elevations, most collectors do not often record elevations with their collection data. A few additional remarks on altitudinal distribution from my own observations are perhaps in order.

In the Great Smoky Mountains *Toxicodendron radicans* subsp. *radicans* occurs at lower elevations but drops out of communities abruptly at 1070 m. Because of its abundance at elevations below 1070 m, the apparent scarcity above that elevation prompted a search for the plant at higher elevations, a search that proved fruitless. *Toxicodendron radicans* subspp. *negundo, pubens,* and *verrucosum* might grow at higher elevations if the requirements of soil, moisture, and community preference were satisfied there also. That is to say, altitude alone probably does not limit their distribution. Indeed, any upper altitudinal limit for these taxa probably is not reached anywhere within their natural ranges.

Toxicodendron radicans subsp. *hispidum* appears to be a true montane plant, having been collected nowhere at elevations less than 1150 meters. In Taiwan, where its distribution is better known than in China proper, it is restricted to the central mountains, and only at the higher elevations. In mainland China, it has been found at elevations estimated at 3450 meters at a latitude of about 25° N. It is perhaps these higher elevations which make the growing conditions more temperate at the lower altitudes.

TABLE 15. ELEVATION SPAN FOR SPECIES OF *TOXICODENDRON* SECT. *TOXICODENDRON*

T. radicans subsp. *radicans*	Sea level to 1070 meters (Smoky Mts.)
T. radicans subsp. *negundo*	Low elevations to 575 meters (Tuscarora Mt., Pa.)
T. radicans subsp. *pubens*	Low elevations
T. radicans subsp. *verrucosum*	Low elevations to 375 meters
T. radicans subsp. *eximium*	300-1700 meters
T. radicans subsp. *divaricatum*	Moderate elevations to 2500 meters
T. radicans subsp. *barkleyi*	Moderate elevations to 2800 meters
T. radicans subsp. *orientale*	Sea level to 1800 meters
T. radicans subsp. *hispidum*	1150-3400 meters
T. diversilobum	Sea level to 1500 meters
T. toxicarium	Low elevations
T. rydbergii	Sea level in Canada to 1150 meters in Oregon to 2500 meters in New Mexico
T. nodosum	Sea level (?) to 1500 meters

Toxicodendron radicans subsp. *orientale* is found at sea level in Hokkaido, but is rare at low elevations farther south, as in the Tokyo valley for example. In southern Honshu, it is more likely to be found in the mountains at moderate elevations. This taxon, however, does appear to have an altitudinal limit. In the Hakone and Nikko regions (35-37° N.) of central Honshu, where the plant has been collected most frequently, it is abundant at elevations of 1200-1300 m., but totally absent at 1800 m. In other words, for these taxa, there appears to be a relationship between latitude and elevation maximum such that the plants will reach higher elevations farther south in their respective ranges.

The relatively low Allegheny and Blue Ridge Mountains appear to act to some degree as a quasi-barrier to gene exchange, since *Toxicodendron radicans* subsp. *negundo* occurs west of these mountains whereas subsp. *radicans* grows east of them with some putative introgression in the mountains. Where *T. rydbergii* occurs in the Appalachians, it is found at the summits of mountains. Whether it is a relict there or is the result of recent invasion is difficult to assess. Where it has been found most frequently at higher elevations has been along road cuts, and it may well be expanding its range southward as habitats open up which satisfy the correct latitude-altitude coefficient.

Toxicodendron rydbergii probably reaches a true elevation limit that is caused by a complex of factors such as length of growing season, frequency of late or early frost, etc., factors which are associated with altitude. It is found no higher than 1150 meters in Oregon and Washington, but grows at elevations up to 2500 meters in New Mexico.

An attempt was made to calculate the coefficient of latitude-elevation maximum for *Toxicodendron rydbergii*, the only member of the species complex for which sufficient data are available to make such calculation. The determinations were based on highest known elevations for this species in Oregon and New Mexico, and checked by collections at high elevations from intermediate localities. The relationship between latitude and maximum elevation is a linear one whose formula is: $K_f = L\ (E_f + 12{,}000)$; where K_f = coefficient of latitude and maximum elevation when elevation is measured in feet, L = latitude in degrees north, and E_f = elevation in feet. Then, substituting for latitude and elevations, values in Oregon and New Mexico and elsewhere: $K_f = 7.2 \times 10^5$. Where elevation is measured in meters, the following holds: K_m = coefficient of latitude and maximum elevation when the elevation is measured in meters and E_m = elevation in meters. Then, again by substitution: $K_m = 2.18 \times 10^5$.

Daubenmire (1954) made a graph of altitude of timberlines in North America plotted against latitude and found a curve which was essentially linear for that part of the world between 35-70°. At more southerly latitudes, the curve changed markedly. For the range of latitudes involved in the distribution of *Toxicodendron rydbergii* (32-52° N.), the computing of a constant for maximum elevation should be more meaningful than for a spread from 0-70° N. Lat. It should follow a straight-line relationship, because the latitude span is all temperate. Furthermore, one is here concerned with the distribution of only one species, therefore involving a single niche, rather than that of an entire life form, i.e., forest trees. Daubenmire (*ibid.*) concludes that

> . . . along the main axis of the North American Cordillera, the elevation of alpine timberline rises steadily at a rate of about 110 m per degree of latitude between 60 and 30°, then declines very gradually to the equator.

Considering that his data include a variety of tree species and deal with highest elevations of species that live far higher than poison-ivy, it is interesting that the altitudinal maximum for *Toxicodendron rydbergii* also rises steadily at a rate of about 109 m per degree!

This close approximation to Daubenmire's figures suggests a biological value of some significance. The altitudinal limit of species distributions and its correlation with latitude might be explored for other plants and also for animals to see if the change of 109-110m/degree is approached.

FIRE

The plants of this complex generally occur in disturbed habitats which are likely to be disturbed repeatedly. The activities of man are important in creating this disturbance, but fire is also a major source of disturbance, especially for the forests in which *Toxicodendron toxicarium* is found. *Toxicodendron radicans*, *T. diversilobum* and *T. rydbergii* are plants which respond favorably to disturbance and are likely to become more abundant following fire, but I have no data to substantiate this supposition. For *T. toxicarium*, on the other hand, there are data to support this claim. In a stand of oak-pine in Lee County, Alabama, Auburn University Forestry Department maintains control-burn plots in which *T. toxicarium* is native. Sets of ten meter square random quadrats were examined in each of two stands — both burned and unburned. The number of shoots per square meter was recorded for each. For ten quadrats in the unburned area, the average was eight shoots/m^2; for ten quadrats in the burned area, the average was 26 shoots/m^2. At another site in Peach County, Georgia, where the most abundant Eastern poison-oak was found of any site investigated, there was ample evidence of burning a few years before (charred stumps, charcoal in the upper soil horizons, etc.). Fire, then, appears to enhance the abundance of *T. toxicarium*.

BIOLOGICAL INTERACTIONS

There are a number of interactions of poison-ivy and the poison-oaks with other plants and with animals. A number of these have been observed first-hand in the field, but most of the following references to such interactions have been derived from the literature. Where references have been consulted, attempts have been made to establish the taxon of *Toxicodendron* involved. Precision is not possible in most instances because the writers have failed to file a voucher specimen of the plant in question in any museum or herbarium, and/or the scientific name which may have been used has been a source of confusion, i.e., *Rhus toxicodendron*.

Among the parasitic fungi, two were found by Rhoads (1918) as examples of wound parasitism: *Polyporus gilvus* and *Irpex lacteus.* A rust genus, *Pileolaria,* is found primarily on *Toxicodendron* and *Rhus* species according to Dr. Joe Hennen (personal communication), having been found infecting *T. diversilobum* and a number of subspecies of *T. radicans* in herbarium material. Arthur (1934) claimed that *Pileolaria toxicodendri*[19] infects *T. radicans* throughout its range. Other fungal infestations are summarized in Table 16.

Insects and other arthropods work on *Toxicodendron* in a variety of ways. One of the chief pollinators of the poison-ivies in Michigan, the Carolinas, New Jersey, and the prairie states is the honey-bee *(Apis mellifera),* which makes a non-toxic honey from its nectar. Presumably the honey-bee is a pollinating vector elsewhere, but has not been specifically recorded as such. Other visitors that appear to transport pollen included other Hymenoptera and

TABLE 16. FUNGI PARASITIC ON *TOXICODENDRON SPP.*

Polyporaceae	*Polyporus gilvus* (Schw.) Fr.	Rhoads, 1918
	Irpex lacteus Fr.	Rhoads, 1918
Pucciniaceae	**Pileolaria brevipes* Berk. and Rav.	Arthur, 1934 and Dr. Joe Hennen, personal communication
Melanconiales	*Cylindrosporium toxicodendri* (Curtis) Dearness	Schwarze, 1917

*Known to parasitize various North American subspecies of *T. radicans*, *T. diversilobum* and the Asiatic subspecies of *T. radicans*, subsp. *orientale* and subsp. *hispidum.*

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[19] *P. brevipes* according to Hennen (personal communication).

several Coleoptera. A number of insect larvae have been observed eating the leaves, and indeed several have been reared to adult stages in the laboratory on leaves solely of this genus. Mr. Murray Hanna reared a nymph of *Clastroptera obtusa* on *T. radicans* subsp. *negundo* leaves in Okemos, Michigan. Dr. Roland L. Fischer reared larvae of *Arge sp.* to adult sawflies on the same taxon from Gull Lake, Michigan. From field observation, he noted damage to individual plants by this larva. Stripped leaflets on which only midribs remain are deposited as vouchers in the Michigan State University Herbarium (MSC). LeConte and Horn (1883) raised a dermestid beetle of the genus *Aspectus* from a tumor on a stem of poison-ivy. Mites were found in leaf galls on specimens of living *T. radicans* subsp. *divaricatum* brought from Mexico City, and determined by Mr. Robert Fouts of the Plant Quarantine Division of the USDA to be *Aculus toxicophagus* (Ewing).

Criddle (1927) observed that *Epipaschia zelleri* larvae made the leaves curl lengthwise to form tunnels. He claimed this larva was the most destructive of all insects to poison-ivy. Larvae of *Lithocelletis guttifinitella* tunnel into the petioles and leaves, making white circular cysts, notable especially as autumn coloration occurs. The pupae then overwinter in the leaves. From specimens deposited in the Michigan State University Entomology Museum, Mr. Julian Donahue has kindly furnished data to the effect that larvae of all members of the subfamily Eutelliinae (family Noctuidae) are known to feed on poison-ivy. Table 17 summarizes the known effects of insects on poison-ivy species.

Some birds eat the fruits of *Toxicodendron radicans* occasionally, and others eat them preferentially (Martin, *et al.*, 1951).[20] It is noted that various flickers, which are

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[20] Although the species of *Toxicodendron* are not enumerated for each bird in the list, one can infer that references to the West Coast must be to *T. diversilobum*, Arizona to *T. rydbergii*, etc. There are certain references which cannot be pinned down precisely, e.g., New England.

fond of ants despite their formic acid content, are partial to fruits of *Toxicodendron*, its fruits comprising up to 25% of their diet. Barrows (1895) suggested that dissemination of the species was accomplished largely by crows. Certainly one may see birds of many kinds as being responsible for the seeds being dropped at the base of trees, telephone poles, and fencerows. There is some indication from anomalous germination tests that I obtained with disseminules of *Toxicodendron* species, that passage through an animal's digestive tract might be needed to break down the waxy and bony layers over the seed to facilitate germination.

Of mammals and their eating of Toxicodendrons, little is known. Although bears, rabbits, and mule deer have been observed browsing the plants (Martin, *et al., loc. cit.*), only the pocket mouse in California has been seen eating seed enough to comprise as much as 25% of the total diet. More than once I have heard of cases of dermatitis in human beings attributed to the skinning of rabbits or squirrels whose stomach contents were largely that of poison-ivy leaves and seeds. No experiments have yet been carried out to test this hypothesis, however. On the other hand, members of the poison-ivy complex are used by small animals in a way other than as food. In localities where ground cover is dense with *Toxicodendron radicans, T. rydbergii*, or *T. diversilobum* the cover and protection they afford are important contributors to the life of rodents which appear to be unaffected by the toxicity of the plants.

PERIODICITY

The flowering times, length of ripening periods, and earliest date of ripened fruits differ among *Toxicodendron rydbergii, T. diversilobum, T. toxicarium*, and the subspecies of *T. radicans*. Among the latter subspecies, there is some correlation of these periods with latitude. Dates discussed here are mean dates of maximum flowering and do not account completely for some precocious and some serotinous flowering. Whether late flowers are a response to photoperiod is not known. Early flowering never precedes the opening of new leaves.

TABLE 17. ARTHROPODS FEEDING ON *TOXICODENDRON SPP.*

LEPIDOPTERA		
Noctuidae	[1]*Paectes oculatrix* (Guenee)	Forbes, 1954, Kimball, 1965
	Eutelia pulcherrima Grote	Forbes, 1954
	[1]*Marathyssa basalis* Walker	Forbes, 1954
Lycaenidae	*Leptotes cassius* theonus (Lucas)	Morgan, 1933; Kimball, 1965
Pyralidae	[2]*Epipaschia zelleri* Grt.	Criddle, 1927
	E. superatalis	Hicks, 1952
Tortricidae	[1]*Episimus argutanus* (Clem.)	Hicks, 1952
	Cacoecia argyrospila Walker	Hicks, 1952
Nepticuliidae	*Nepticuli rhoifoliella* Braun.	Forbes, 1960
	Lithocelletis guttifinitella Clemens	Forbes, 1960
Gracilariidae	*Gracilaria rhoifoliella* Chambers	Forbes, 1960
HYMENOPTERA		
Argidae	[1]*Arge humeralis* (Beauv.)	Frank Craighead, personal communication

TABLE 17. — *Continued*

DIPTERA		
Cecidomyiidae	[3]*Lasioptera sp.*	Frank Craighead, personal communication
Cecidomyiidae	*Dasyneura rhois*	Felt, 1928
COLEOPTERA		
Scarabaeidae	*Phyllophaga ulkei* Smith	Howden, Howden, and Ritcher, 1951
Melolonthidae	*Serica vespertina* Gyllenhal	*ibid.*
	Diplotaxis bidentata LeConte	*ibid.*
Dermestidae	*Aspectus hispidus* Melsh	Hicks, 1955, LeConte and Horn, 1883
Chrysomelidae	*Pachybrachys tridens* (Melsh.)	MSU Entomology Museum data
Ipidae	*Pityophthorus rhois* Swaine	Frank Craighead, personal communication
Cerambycidae	*Astylopsis macula* (Say)	Beal and Massey, 1945
Cerambycidae	*Leptostylus albescens*	*ibid.*
Curculionidae	*Cryptorhynchus fuscatus* Lec.	*ibid.*
Scolytidae	*Xyleborus pecanis* Hopk.	*ibid.*

TABLE 17. — *Continued*

Scolytidae	*X. affinis* Eichh.	*ibid.*
Curculionidae	*Madarellus undulatus* (Say)	Blatchley and Leng, 1916
Scolytidae	*Hypothenemus toxicodendri* Hop.	*ibid.*
Scolytidae	*Pityophthorus consimilis* Lec.	*ibid.*
BORER	*Oherea ocellata* Haldeman	Frank Craighead, personal communication
Diaspididae	*Aspidiotis sp.*	McNair, 1923
Clastropteridae	*Clastroptera obtusa*	Murray Hanna, personal communication
Aphididae	*Carolinaia rhois* Tissot	Tissot, 1928
MITES		
Eriophyidae	[1]*Aculus toxicophagus* (Ewing)	Robert Fouts, personal communication

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[1] Larvae on leaves.

[2] Considered by some to be the most destructive insect to the poison-ivy plant.

[3] Galls on aerial roots.

Time of flowering for *Toxicodendron radicans* subsp. *radicans* begins at the southern tip of Florida at some time between the end of January and the middle of February. The flowering date appears progressively later toward the north, arriving in late March and early April in northern Florida, mid-May in the Carolinas, early June in the middle Atlantic States, and the first week in July at the north-

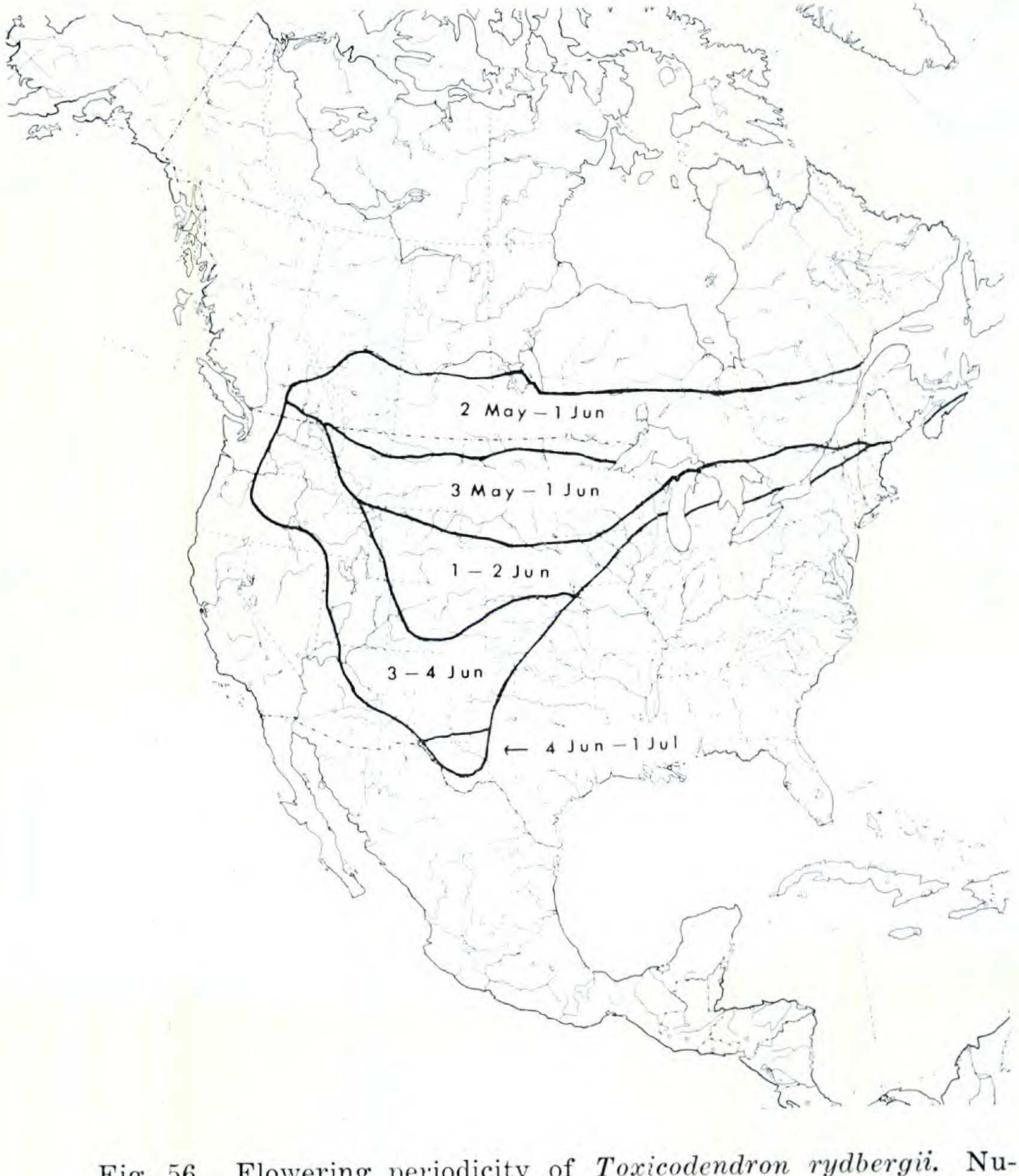

Fig. 56. Flowering periodicity of *Toxicodendron rydbergii*. Numerals refer to the *week* of the month in question.

ern limit of its range in southern Maine. Flowering periods for *T. rydbergii* begin the second week in May at the southern end of its range, and progress to the end of June and early July at its northern limit. For *T. radicans* subsp. *negundo*, the span is from mid-April to the latter part of June. Figs. 56 and 57 show the flowering date progression for these taxa.

Fig. 57. Flowering periodicity of *Toxicodendron radicans* subsp. *negundo*. Numerals refer to the *week* of the month in question.

In Japan, *Toxicodendron radicans* subsp. *orientale* flowers in late May in Kyushu and Shikoku, between the second week in June in southern Honshu to the first week in July for northern Honshu. In Hokkaido, the plant flowers during the last two weeks in June except for the Rishiri Islands, where it flowers early in July. In the Kuriles and Sakhalin, it flowers between the last week in June and the first week in August. Subspecies *hispidum* appears to flower in Taiwan at the end of April or in early May, and on the mainland of China during the last two weeks of May.

Within *Toxicodendron radicans* subsp. *divaricatum* there appear to be two periods of flowering maxima, one in April and May, and one in early to mid-August or even early September. There seems to be no geographical nor photoperiodic pattern to the flowering cycle. Even within a given area (e.g., Michoacán) flowering has been reported in early April, early May, early June, and late August from different populations. Further study might reveal correlations with rainfall or some other ecological factor, but for now, these differences are attributed only to local population variation. Subspecies *barkleyi* shows a similar spread of flowering dates, except that any secondary flowering period is earlier than that for subsp. *divaricatum* (early July rather than August or September). One Jalisco population, however, is recorded as flowering abundantly in November.

Flowering periods for *Toxicodendron diversilobum* shift northward with the season, beginning in late March in Baja California, commencing later in northern California and Oregon, and finishing the last week of May to the second week in June in Washington and British Columbia (Fig. 58). For *T. toxicarium*, on the other hand, a simple geographic pattern can be established. Fig. 58 also shows the flowering dates for this species.

Length of time required for fruits to ripen also differs with latitude for several taxa. For others, there are too few data to determine these figures precisely. Fruits are judged to be ripe when the exocarp is no longer green, no longer shrivels in the drying of herbarium specimens, and becomes brittle, separating from the mesocarp. At the

Fig. 58. Flowering periodicity of *Toxicodendron diversilobum* and *T. toxicarium.* Numerals refer to the *week* of the month in question.

southern tip of Florida, fruits ripen in *Toxicodendron radicans* subsp. *radicans* in three months, but in northern Florida, this ripening extends to four months. The ripening then shortens with increase in latitude to only two months in southern New England at the northern end of the range. Between central Florida and Maine, this average ripening difference is shortened by roughly four days per degree of latitude (Fig. 59).

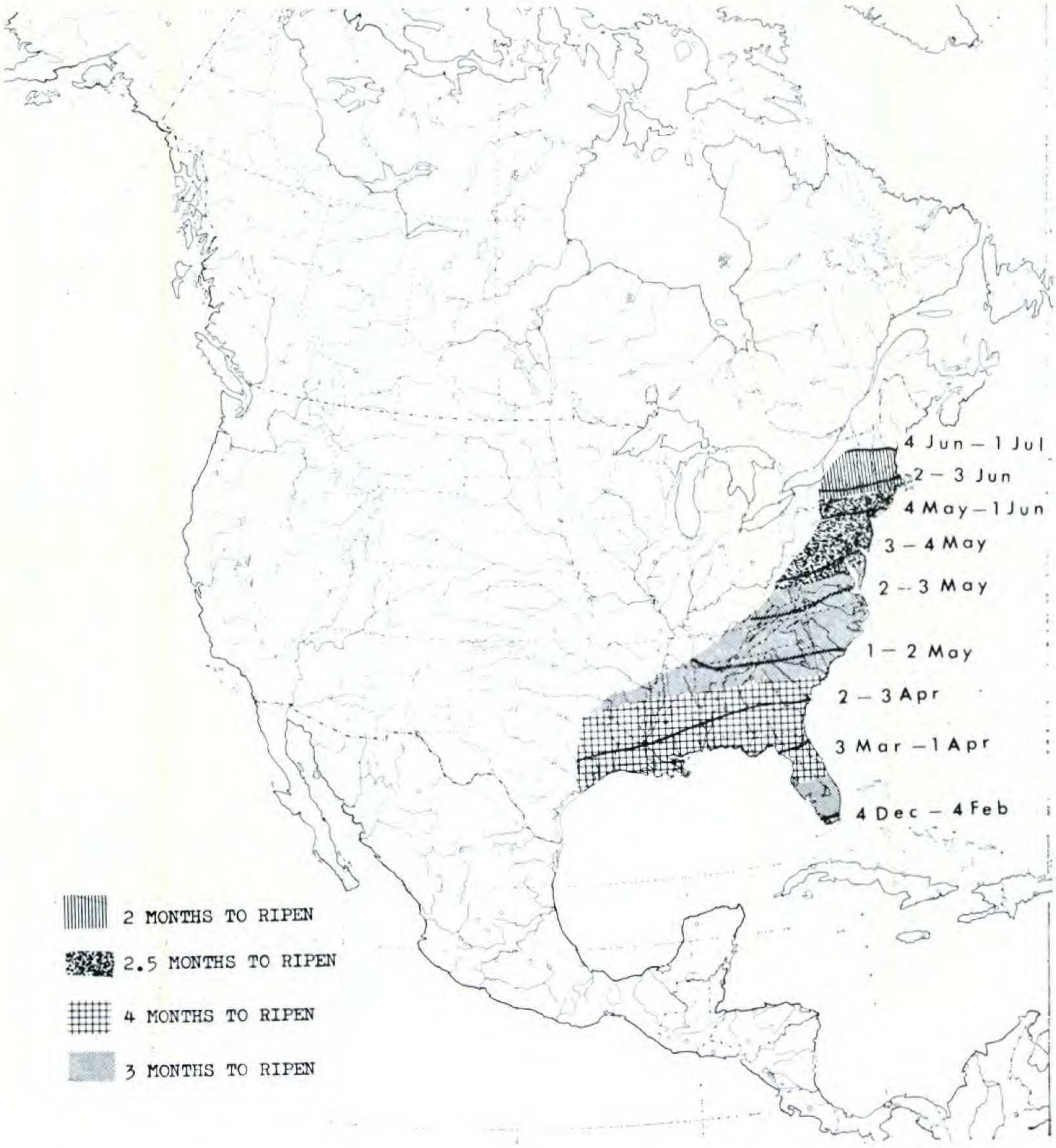

Fig. 59. Flowering and fruiting periodicity of *Toxicodendron radicans* subsp. *radicans*. Numerals refer to the *week* of the month in question. Shading refers to the length of time required for fruit ripening.

The span of latitude for subsp. *negundo* is smaller than that of subsp. *radicans*, so there is not so noticeable a difference in ripening time with changes in latitude. Throughout the range, except for upper New York (two months) and northern Texas (four months), the ripening time is about three months. Although extensive data are lacking for subsp. *orientale*, it appears that two months are required for ripening in Honshu, but only one and a half months in Hokkaido and north. No fruiting specimens from Kyushu or Shikoku have been seen.

Ripening of fruits of *Toxicodendron radicans* subsp. *divaricatum* requires about three months. The ripening time lengthens to four months in Baja California, and shrinks to two months in Sonora. Because of the divergence of flowering times, precise data for more than two or three localities were not obtainable. With what little data could be trusted from which to draw inferences about ripening time in subsp. *barkleyi*, it appears to require the longest period of all — up to four and a half to five months. Again from sparse data, one may estimate ripening time for subsp. *eximium* at one month, for subsp. *pubens* at three months, and for subsp. *hispidum* at two months.

Toxicodendron toxicarium requires from six to nine weeks for ripening of fruit, with no particular geographical pattern to the variations. *Toxicodendron diversilobum* requires eight to ten weeks for ripening with the shorter period in northern California north to Canada and the longer period in central California south to Baja California.

Toxicodendron nodosum has been collected more times in flowering stage than in fruiting condition. Flowering specimens have been collected from Java in July, August, and September, from Malaya in September (Larut) and December (Perak), and from Sarawak in June. Reliable ripening dates are not available, but what little data there are suggest that it takes about two months for the seeds to ripen.

In summary, one may say that the fruits of most members of the poison-ivy complex are ripe by the end of August or first part of September with three exceptions: (1) the early flowering (December to February) populations will be ripe by early summer; (2) the serotinous flowering populations will not produce ripe fruit until late in the calendar year if at all; and (3) *Toxicodendron nodosum* has different flowering and fruiting periods in different regions.

REPRODUCTIVE BIOLOGY

Most of the reproduction of poison-ivy and its allies is vegetative, enabling a single disseminule to grow to cover up to an acre of land. New populations, of course, are begun by seed. Cuttings do not fare well and are very susceptible to damping off. Only three cuttings grown in the laboratory (out of sixty-three attempted) were still alive three months later. None survived a winter out of doors in experimental plots in southern Michigan. These cuttings represented seven taxa (*Toxicodendron diversilobum, T. rydbergii, T. toxicarium, T. radicans* subspp. *radicans, negundo, divaricatum,* and *verrucosum*).

Germination is epigeal. The cotyledons are still borne within the tough endocarp and testa until after the hypocotyl emerges. A few never fully emerge, and die. The root hairs are brown. In those taxa wherein it was tested, viability is generally good to at least six years — no longer tests were run — but seeds require special treatment for germination.

A series of tests were set up to determine germination requirements. Seeds were gathered from 35 sources representing eight taxa. One hundred seeds of each population were placed in petri dishes on wet filter paper, replicated four times for each treatment. One treatment tested immediate germination without special treatment; another tested germination after six weeks of moist storage at 1° C. Results were tabulated up to four weeks after the start of the germination at room temperature, at which time the experiment was terminated.

Only seeds from populations of *Toxicodendron radicans* subsp. *radicans* in Gainesville, Florida, and in Bermuda germinated without after-ripening chill. No germination was recorded at all from seeds of *T. toxicarium, T. radicans* subsp. *barkleyi*; little germination occurred with seeds of *T. rydbergii, T. radicans* subsp. *verrucosum* and *T. diversilobum.* Germination results ranging from 10.75% to 62% were obtained for *T. radicans* subsp. *negundo,* and between 3.5% to 81.75% for *T. radicans* subsp. *radicans* (mean was

40%). Seeds produced during four seasons were gathered from one population of *T. radicans* subsp. *radicans* at Island Beach State Park, New Jersey (1955, 1956, 1958, and 1959). The average germination remained essentially the same, but appeared to increase very slightly with age. Table 18 gives the germination results. In order for conclusive growth studies to be possible in future experiments, the problem of germination must be solved, especially for the taxa for which no germination was effected. Scarification with acid, sandpaper, or fire, or removal of the mesocarp before testing were not tried.

TABLE 18. GERMINATION OF *TOXICODENDRON* SEEDS

Trials followed six weeks of moist storage at 1° C. Results are based on 100 seeds per trial and are recorded in per cent germination

	Replicate				Mean
	1	2	3	4	
T. radicans subsp. *radicans*					
Cape Hatteras, N. C.	27	43	54	46	42.5
Gainesville, Fla.	70	65	65	51	60.25
Chapel Hill, N. C.	17	10	19	21	16.75
Sapelo Island, Ga.	25	26	21	28	25.0
Bermuda	64	59	54	49	56.5
Williamstown, Mass.	13	29	21	16	19.75
Cape Charles, Va.	66	72	86	66	72.5
Middlebush, N. J.	95	72	77	83	81.75
Columbia, S. C.	4	6	3	1	3.5
Island Beach, N. J.					
1955	59	42	44	43	47.0
1956	21	29	35	39	31.0
1958	34	34	37	40	36.25
1959	33	36	34	29	33.0

TABLE 18. — *Continued*

	Replicate				Mean
	1	2	3	4	
T. radicans subsp. *negundo*					
East Lansing, Mich.	60	67	62	59	62.0
Haslett, Mich.	57	49	61	54	55.25
Norman, Okla.	10	14	10	9	10.75
T. radicans subsp. *verrucosum*					
Austin, Texas	1	2	6	3	3.0
T. radicans subsp. *orientale*					
Nikko, Japan	0	0	0	0	0
T. radicans subsp. *barkleyi*					
Galeana, Mexico	0	0	0	0	0
Huehuetenango, Guatemala	0	0	0	0	0
T. rydbergii					
Beulah, Mich.	0	1	1	0	0.5
DeTour, Mich.	0	0	0	0	0
Kah-Nee-Ta Hot Spring, Ore.	3	5	1	3	3
Saugatuck, Mich.	1	0	4	1	1.5
Lake Itasca, Minn.	0	0	0	1	0.25
T. diversilobum					
Berkeley, Calif.	0	0	1	3	1.0
Sacramento, Calif.	3	6	0	2	2.75
Placerville, Calif.	0	1	0	0	0.25
Trail, Ore.	1	0	1	0	0.5
Corvallis, Ore.	0	3	1	0	1
The Dalles, Ore.	0	0	0	0	0
Kalama, Wash.	0	0	0	0	0
T. toxicarium					
Morehead City, N. C.	0	0	0	0	0
Gaston, S. C.	0	0	0	0	0
Gainesville, Fla.	0	0	0	0	0
Bastrop, Texas	0	0	0	0	0

Seeds of a number of populations were weighed to determine if differences existed between taxa in seed weight. Fifty disseminules were weighed, each being an intact seed with endocarp and mesocarp attached. The total weights are tabulated in Table 19. The heaviest propagules are those of *Toxicodendron diversilobum*. Those of *T. toxicarium* and of *T. rydbergii* are next heaviest. Those of *T. radicans* subsp. *radicans* and subsp. *verrucosum* are the lightest. Putative hybrid "seeds" of *T. diversilobum* × *T. rydbergii* in the Columbia River Valley of Oregon were heavier than those of any pure species measured, averaging 2.38 g/50 seeds.

Community Specificity for *Toxicodendron Toxicarium*

The range of community types in which the various taxa of the poison-ivy complex grow is generally broad except for *T. toxicarium*. Other than for a very few unusual cases, its community preference is so marked that it can be readily spotted from a moving automobile. Its greatest abundance is in a sandhills type of vegetation typical of the Carolina fall-line sandhills, but common elsewhere on the Coastal Plain. This habitat may be described simply as a fairly open, dry, savanna woodland of oak and pine (more oak than pine). In Oklahoma and parts of Texas beyond the range of pine, most other components of the community are nonetheless present. The woods are usually disturbed, often by fire. They are never very old, generally less than fifty years. The wide spacing of the trees allows for a great deal of light to reach the herb layer where *T. toxicarium* grows. The soil is excessively drained; often the degree of dryness is emphasized by the presence of lichens such as *Cladonia cristatella* on the surface. The herb layer always has bunch and wire grasses: *Andropogon*, *Stipa*, or *Aristida*, and a variety of legumes: *Clitoria mariana*, *Petalostemon*, *Stylosanthes*, *Tephrosia*, and *Lespedeza* to mention a few of the more important. The acid litter of oak and pine has formed acid soils in which *Vaccinium* and occasionally *Gaylussacia* grow well. *Crataegus uniflora* and *Cnidoscolus*

TABLE 19. SEED WEIGHTS OF *TOXICODENDRON* SPECIES

Values recorded are in grams for fifty randomly-chosen seeds from a given population

Population	*T. rydbergii*	*T. radicans* subsp. *radicans*	*T. radicans* subsp. *verrucosum*	*T. radicans* subsp. *negundo*	*T. diversilobum*	*T. toxicarium*
1	1.14	1.2	0.83	0.97	1.77	1.40
2	1.38	1.71		1.17	2.05	1.70
3	1.34	0.53		0.90	1.54	1.57
4	1.20	0.55		1.45	1.64	
5	1.30	0.55			1.74	
6	1.22	0.75			1.63	
7	1.15	0.92				
8	1.52	0.92				
9	1.43					
Mean	1.297	0.891	0.83	1.12	1.728	1.56
Range	1.14-1.52	0.53-1.71		0.90-1.45	0.77-2.05	1.40-1.70

stimulosus are additional faithful components of this association. The general sandhills type of vegetation of which this association is a part has been described in detail by Wells and Shunk (1931) and Duke (1961). The Florida component of this formation is detailed by Laessle (1958) and Monk (1960). The chief associates of *T. toxicarium*, from my collections, are listed in Table 20.

Since the environments where *Toxicodendron radicans* is generally found are those which do not support *T. toxicarium*, an attempt was made to examine intensively the community preference for the latter to see what was specialized about its niche. A search was made for a habitat on the Atlantic Coastal Plain where both species grew close together and, if possible, grow in the same community. Two such communities were found that fit the objective well, plus a marginal third. These three are discussed herein and in the section on soils analysis.

One of the two major communities examined is in northern Florida in an area described as the San Felasco region about 12 miles NW of Gainesville in Alachua County (T. 9S., R. 19E., Sec. 21, 1.7 miles off Devil's Millhopper Road). It is best described as intermediate between hammock and sandhills vegetation and has been studied by Monk (1960) as he explored the transition between sandhills and hammock over a gradient of soil and vegetational change. An area of somewhat more than an acre was found near the site studied by Dr. Monk, in which both *Toxicodendron toxicarium* and *T. radicans* subsp. *radicans* grew together abundantly, i.e., an extensive tract of essentially transitional vegetation. The soils of the transition zone have a higher percentage of finer particles than the soils in which *T. toxicarium* generally grows, and are higher in calcium content than those where this species is usually common. On the other hand, it is probably the fine particles and increased calcium and other nutrients, especially in the upper soil horizons where the roots are concentrated, which enables *T. radicans* to survive. As Monk *(ibid.)* notes, this transition zone has species of both sandhills and hammock

TABLE 20. ASSOCIATES OF TOXICODENDRON TOXICARIUM IN SANDHILLS VEGETATION

	Georgia	Florida	Carolinas	Texas	New Jersey
Pinus palustris	x	x			
P. echinata		x			x
P. taeda	x	x	x	x	
Juniperus virginiana				x	
Myrica cerifera	x	x	x		x
Carya pallida				w	x
C. cordiformis			x		
C. tomentosa		x			
C. glabra		x	w		
Quercus alba					x
Q. falcata	x	x	x		
Q. incana	x		x		n
Q. laevis	x	x	x	w	n
Q. lyrata		x	x		
Q. marilandica	x		x	x	x

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Q. nigra		x	x		n
Q. stellata (incl. var. margaretta)	x		x	x	x
Eriogonum tomentosum	x	x	x	w	n
Polygonella americana			x		
Froelichia floridana	x	x	x	w	n
Magnolia virginiana			x		
Asimina angustifolia		x	x	w	
A. incana	n	x	n	w	n
Stipulicida setacea			x	w	n
Sassafras albidum		x	x		x
Crataegus uniflora	x	x	x	w	
Prunus caroliniana			x	w	n
P. umbellata		x		w	n
Aronia arbutifolia		x		w	
Rubus cuneifolius		x		w	

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
R. trivialis		x	x		
Baptisia leucantha		x		w	
Cassia fasciculata	x	x		x	
C. nictitans	x		x		
Centrosaema virginianum			x	x	
Clitoria mariana	x	x		x	
Crotolaria rotundifolia		x		x	
Desmodium canescens			x		
Galactia floridana		x		w	
Lespedeza hirta	x		x		
L. striata	x				
Lupinus villosus		x			
Petalostemon pinnatum	x			w	n
Phaseolus sinuatus	x	x		w	n
Rhynchosia simplicifolia var. tomentosum		x	x	w	n

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Stylosanthes biflora	x	x	x		
Tephrosia virginiana	x	x	x		
Polygala grandiflora	x	x		w	n
Cnidoscolus stimulosus	x	x	x	x	n
Croton argyranthemus	x		x		
C. capitatus	x		x		
Euphorbia corollata			x		
Stillingia sylvatica	x	x			n
Ceanothus americana			x		
Rhus copallina	x	x			
Ilex opaca		x	x		
Vitis cordifolia	x		x	w	
V. mustangensis var. linescumii				x	
Hypericum hypericoides			x		
Helianthemum georgianum	x	x			

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Lechea maritima	x		x	w	
L. villosa			x		
Oxalis dillenii		x			
Eryngium yuccifolium var. synchaetum	x				
Chimaphila maculata			x		
Gaylussacia frondosa			x	w	
G. dumosa			x	w	
Vaccinium arboreum			x		n
V. stamineum		x	x	w	
V. corymbosum	x		x	w	x
V. tenellum		x	x		
V. vacillans			x	w	
Polypremum procumbens	x				
Osmanthus americanus		x		w	
Gelsemium sempervirens	x	x	x	w	n

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Asclepias tuberosa	x	x			x
A. verticillata	x				
Phlox nivalis	x			w	x
P. floridana		x		w	
Callicarpa americana				x	n
Scutellaria integrifolia var. glandulosa	x	x		w	
Salvia lyrata	x	x			
Trichostema dichotomum					x
Penstemon australis		x	x	w	n
Verbena caroliniana		x		w	
Ruellia caroliniensis		x			x
Galium pilosum	x		x		
Diodia teres	x		x		
Berlandiera tomentosa	x	x		w	
Chrysopsis graminifolia			x		

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Elephantopus tomentosus	x	x	x	w	n
Eupatorium hyssopifolium	x		x	w	
Helenium tenuifolium			x	w	
Hymenopappus scabiosaeus		x			
Krigia biflora		x		w	
Pyrrhopappus carolinianus		x			
Senecio smallii	x	x	x		
Silphium compositum	x	x	x	w	n
Solidago brachyphylla		x			
S. bootii			x		n
S. odora			x		
S. tortifolia			x		
Tetragonotheca helianthoides		x		w	
Vernonia angustifolia	x	x		w	n
V. texana				x	

TABLE 20. — *Continued*

	Georgia	Florida	Carolinas	Texas	New Jersey
Aristida lanosa	x			x	x
A. stricta	x	x	x	w	n
Andropogon scoparius	x		x	x	x
A. ternarius	x	x	x		x
Danthonia sericea			x	w	
Panicum potoricense			x		n
P. mutabile			x		
P. repens		x			
Cyperus retrofractus	x				
C. ovularis			x		
Smilax glauca			x	x	
Juncus secundus			x	w	
Nolina georgiana	x				
Polygonatum commutatum			x	w	
Sisyrinchium atlanticum		x			
S. fibrosum			x		n
Spiranthes grayi				x	

x = species collected, voucher deposited at MSC.
n = species reaches its northern limit south of New Jersey.
w = species reaches its western limit east of Texas.

communities, although some species which prefer extremes of each type are absent.

A clue to the ecological requirements of *Toxicodendron toxicarium* comes from a gradient study north of Columbia, Richland County, South Carolina (Fig. 60). A 110-meter transect was run along a 5% slope from a heavy textured soil where *T. radicans* subsp. *radicans* was frequent, to a sandhills community on sand where *T. toxicarium* was plentiful. Only in the middle of the transect did both species occur together, and there they occurred abundantly. Although the two plants flowered at the same time and had the same pollinating vector (honey-bee), there was evidence of only one individual which could be classed as a putative hybrid.

The vegetation analysis was made by selecting quadrats of ten meters on a side along the transect line, alternating sides of the base line. In these quadrats, all tree species were recorded in terms of diameter at breast height (dbh), and the measurements totaled for the quadrat. Two quadrats within the larger 100 m^2 quadrat were selected in which stems of all shrubs were counted. Four smaller quadrats were selected, nested within the 100 m^2 quadrats in which per cent cover of the plants in the herb layer was estimated. The tables which follow (21-23) show a gradual shift to the north from a hardwood forest to a sandhills oak-pine scrub, with lessening density of trees. Calcium content of the upper soil horizon drops and the soil texture becomes lighter; there is more leaching in the A horizon. Further, the species numbers become fewer. Loblolly pine occurs in each quadrat, but becomes less abundant (as do all tree species) upward along the gradient. In short, as measured up the gradient, the vegetation changes to one more characteristic of the typical vegetation in which *Toxicodendron toxicarium* may be found. Due to the plants' abundance, there is no lack of seed source for each extreme of the gradient to receive disseminules from the other end of the gradient. The differential in distribution of the taxa must involve factors in the soil and/or associated vegetation.

Fig. 60. Gradient through forest in South Carolina. A. View into mesic hardwood-pine forest on loamy sand. Poison-ivy is abundant. B. Middle of gradient where poison-ivy and poison-oak overlap. C. Dry end of gradient on coarse, shallow sand. Sandhills type of vegetation. Poison-oak is abundant.

TABLE 21. TREES FOUND ON TRANSECT FROM HARDWOOD FOREST TO SANDHILLS COMMUNITY, SOUTH CAROLINA. TRANSECT RUNS SOUTH-NORTH ALONG A DECREASING SOIL MOISTURE GRADIENT, COLUMBIA, RICHLAND COUNTY, SOUTH CAROLINA, 12 MAY 1961

Tree species are recorded if they occurred in 10 × 10 meter quadrats, and are totaled in dbh. for all trees within the quadrat and are expressed in sq. dm. Quadrat 1 is in hardwood forest; quadrat 10 is in sandhills vegetation

Species	Quadrats									
	1	2	3	4	5	6	7	8	9	10
Carya tomentosa	0.40								0.65	
Liquidambar styraciflua	0.05			0.08	0.45		0.14			
Cornus florida	0.08		0.31				0.30			
Pinus taeda	10.00	3.92	7.93	8.97	4.56	3.78	7.60	8.06	3.04	5.06
Acer rubrum		0.12		0.164						
Ilex opaca	0.1									
Quercus falcata		0.14								
Ceanothus americana	0.158			0.13						
Rhus copallina				0.06						
Quercus nigra						0.05				

TABLE 21. — *Continued*

Species	Quadrats									
	1	2	3	4	5	6	7	8	9	10
Prunus serotina							0.15		0.05	
P. caroliniana							0.11			
Quercus stellata						0.06				
Magnolia virginiana								0.05		
Quercus marilandica									0.90	

TABLE 22. SHRUBS FOUND ON TRANSECT FROM HARDWOOD FOREST TO SANDHILLS COMMUNITY, SOUTH CAROLINA. TRANSECT RUNS SOUTH-NORTH ALONG A DECREASING SOIL MOISTURE GRADIENT, COLUMBIA, RICHLAND COUNTY, SOUTH CAROLINA, 12 MAY 1961

Shrub species are measured by numbers of stems in 2 × 5 m quadrats, nested inside 10 × 10 m quadrats laid out for tree species measurements

Species	Quadrats										
	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a
Toxicodendron radicans subsp. radicans	7			1	2			6	31	19	7
Vitis cordifolia	32			4	14	2	27	21	19	11	16
Smilax rotundifolia	1							5	3	5	
Gelsemium sempervirens	2				3			2	2	3	2
Crataegus uniflora	2		2								
Acer rubrum		3	8						1		
Magnolia virginiana		3	8						1		
Vaccinium stamineum											
Smilax glauca			4		1		5	17			
Carya tomentosa			1					1			

TABLE 22. — *Continued*

Species	Quadrats										
	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a
Prunus caroliniana			1								
P. serotina				2		2			3		
Ampelopsis arborea				4	6	4	1				
Quercus nigra								1			3
Cornus florida								1			
Quercus lyrata								1	1		
Toxicodendron toxicarium								1		4	25
Rubus trivialis								2			
Quercus stellata									1		
Parthenocissus quinquefolia									3		
Rhus copallina											1
Quercus falcata											
Hypericum hypericoides											
Cassia nictitans											
Pinus taeda											
Vaccinium arboreum											
Liquidambar styraciflua											
Quercus marilandica											

TABLE 22. — *Continued*

Species	Quadrats										
	6b	7a	7b	8a	8b	9a	9b	10a	10b	11a	11b
Toxicodendron radicans subsp. radicans	4	19	2								
Vitis cordifolia	12		2	2	2		11				
Smilax rotundifolia		1	2						2	4	1
Gelsemium sempervirens		5		2	8						
Crataegus uniflora	1										
Acer rubrum											
Magnolia virginiana											
Vaccinium stamineum	3				3	1	4	4	1	3	
Smilax glauca											
Carya tomentosa											
Prunus caroliniana		2	4	1	3		2	1		2	
P. serotina	2		2		1						
Ampelopsis arborea											
Quercus nigra	2		1						2		

TABLE 22. — *Continued*

Species	Quadrats										
	6b	7a	7b	8a	8b	9a	9b	10a	10b	11a	11b
Cornus florida											
Quercus lyrata		1	4		4	1					
Toxicodendron toxicarium	6		4	2	8	5	3	16	18	11	19
Rubus trivialis			1								
Quercus stellata											
Parthenocissus quinquefolia	1										
Rhus copallina											
Quercus falcata	1	1									
Hypericum hypericoides	3	2									
Cassia nictitans	3										
Pinus taeda		2								2	
Vaccinium arboreum							3				
Liquidambar styraciflua							1				
Quercus marilandica							2				

TABLE 23. HERBS FOUND ON TRANSECT FROM HARDWOOD FOREST TO SANDHILLS COMMUNITY, SOUTH CAROLINA. TRANSECT RUNS FROM SOUTH-NORTH ALONG A DECREASING SOIL MOISTURE GRADIENT, COLUMBIA, RICHLAND COUNTY, SOUTH CAROLINA 12 MAY 1961

Herb species are measured by per cent cover in 0.5 × 2.5 m quadrats inside 10 × 10 m quadrats laid out for tree species measurements. t = trace, less than 1 per cent

Species	Quadrats											
	1a	1b	1c	1d	2a	2b	2c	2d	3a	3b	3c	3d
Vitis cordifolia	32	38	18	2	5	12	30	31	26	29	18	5
Gelsemium sempervirens	t	2	5	1	9	2	5	1	8	11	14	10
Silphium compositum	1	4	2									
Litter	60	65	75	80	70	85	66	75	65	63	51	85
Toxicodendron radicans subsp. radicans	9	4	3			1		1				
T. toxicarium	1	2										
Tree		3									4	
Rubus trivialis		t	t									
Poa sp.		t					t					
Magnolia virginiana			3									
Mitchella repens			t	t	t	t	1	3		2	1	1
Parthenocissus quinquefolia			2				t					
Acer rubrum				4	5	3						
Vacinnium tenellum				4	2							

TABLE 23. — *Continued*

Species	Quadrats											
	1a	1b	1c	1d	2a	2b	2c	2d	3a	3b	3c	3d
Smilax glauca				t	1		4			t	t	1
Carex sp.				t								
Senecio smallii					t							
Panicum mutabile				t		1						
Smilax rotundifolia						8	4			1		2
Lespedeza hirta						t6		1	1			
Quercus falcata						t						
Oxalis dillenii							t					
Prunus serotina								2				
Ampelopsis arborea									1	t	t	4
Euphorbia corollata								3	1			
Vaccinium stamineum											2	
Quercus lyrata											1	
Desmodium canescens												
Cornus florida												
Tephrosia virginiana												
Ceanothus americana												

TABLE 23. — *Continued*

Species	Quadrats									
	4a	4b	4c	4d	5a	5b	5c	5d	6a	6b
Vitis cordifolia	13	55	45	12	26	23	28	10	11	15
Gelsemium sempervirens	3	5	2	1	1	2	3	1	3	t
Silphium compositum										
Litter	80	36	50	70	60	64	62	67	60	40
Toxicodendron radicans subsp. radicans	t		1	2	5	31	25 =	11	2	t
T. toxicarium							13	7	19	38
Tree	t		15	1	4		2			
Rubus trivialis		1				4			1	
Poa sp.										
Magnolia virginiana										
Mitchella repens								4		
Parthenocissus quinquefolia			t	1	1	3	2			
Acer rubrum										
Vacinnium tenellum										
Smilax glauca	3	2	2	2	2	5	16	6	3	

TABLE 23. — *Continued*

Species	Quadrats									
	4a	4b	4c	4d	5a	5b	5c	5d	6a	6b
Carex										
Senecio smallii										
Panicum mutabile							1			
Smilax rotundifolia	2	t	2	6	7			1		
Lespedeza hirta										
Quercus falcata										
Oxalis dillenii										
Prunus serotina										
Ampelopsis arborea		2	2							
Euphorbia corollata										
Vaccinium stamineum										
Quercus lyrata		t								
Desmodium canescens		1								
Cornus florida			2							
Tephrosia virginiana							2		t	
Ceanothus americana										

TABLE 23. — *Continued*

Species	Quadrats											
	6c	6d	7a	7b	7c	7d	8a	8b	8c	8d	9a	9b
Vitis cordifolia	40	60	48	56	8	65	20	45	38	9	21	18
Gelsemium sempervirens	1	2	t	2	1	2	1	3	4	1	5	6
Silphium compositum												
Litter	45	25	26	24	85	80	60	45	45	78	60	60
Toxicodendron radicans subsp. radicans		3	7	6								
T. toxicarium	13				2	12	5			6	4	12
Tree	3	5	2	10			8			t		
Rubus trivialis						2			4	t	2	
Poa sp.												
Parthenocissus quinquefolia		3										
Smilax glauca			1	3			2					
Senecio smallii							1					
Lespedeza hirta	t		1	6								
Quercus falcata												
Prunus serotina												

TABLE 23. — *Continued*

Species	Quadrats											
	6c	6d	7a	7b	7c	7d	8a	8b	8c	8d	9a	9b
Stylosanthes biflora	1		t			3		1	3	2	t	1
Euphorbia corollata	t							1	2	1		
Ceanothus americana	2				t							
Pinus taeda		t		t	1		t					t
Quercus nigra		1					2					
Q. lyrata			5			1						
Desmodium canescens			8		1							
Polygonatum commutatum			2		1		t					
Galium pilosum				t	t	t						1
Danthonia sericea					t							
Prunus caroliniana					1			3		1		
Vaccinium stamineum						2		2				4
Tephrosia virginiana							t					
Quercus marilandica												
Andropogon ternarius												

TABLE 23. — *Continued*

Species	Quadrats									
	9c	9d	10a	10b	10c	10d	11a	11b	11c	11d
Vitis cordifolia	14	9	3	1		2				
Gelsemium sempervirens	5	12	3	4	2					
Silphium compositum	8		3				2			
Litter	70	55	30	65	88	90	75	75	92	90
Toxicodendron radicans subsp. radicans										
T. toxicarium	2		29	8	13	5		1		
Tree	t									
Rubus trivialis			2			1				
Poa sp.										
Parthenocissus quinquefolia										
Smilax glauca	4	30	11							
Senecio smallii			8	1	6	1	t	4	1	3
Lespedeza hirta	1						t			
Quercus falcata						2				
Prunus serotina										

TABLE 23. — *Continued*

Species	Quadrats									
	9c	9d	10a	10b	10c	10d	11a	11b	11c	11d
Stylosanthes biflora	t	1	3				1	1 =	t	1
Euphorbia corollata										
Ceanothus americana										
Pinus taeda							1			
Querycus nigra										
Q. lyrata										
Desmodium canescens										
Polygonatum commutatum										
Galium pilosum										
Danthonia sericea							t		t	
Prunus caroliniana	2									
Vaccinium stamineum		t		2	14		6	1		4
Tephrosia virginiana										
Quercus marilandica		13	2			1	11		2	1
Andropogon ternarius				t		t		t	1	t

SOIL STUDIES

A number of soil and site analyses were made to determine if members of the poison-ivy complex demonstrate any soil requirement specificity. A total of 38 soil pits was dug and samples of each horizon were brought back to the laboratory for analysis. These samples represented the soils in which nine taxa grew, of which four seemed to show some very specific requirements.

Each horizon was analyzed for texture, pH, and major nutrients available in parts per million. Soil texture was analyzed by the hydrometer method (Bouyoucos, 1936) and verified by touch. pH tests were run on a Beckman pH meter against a known phosphate buffer. The concentration of P, K, Ca, and Mg available was determined by the Soil Testing Laboratory of Michigan State University. From these data, soil profile information was synthesized and the profiles identified as well as could be done with available soil survey information. No soil data are available for the Asiatic taxa, except that it is known from herbarium label data that *Toxicodendron nodosum* has been found only on shallow limey soils. No data are available for the soils in which *T. radicans* subsp. *divaricatum* grows.

Although soil profiles were studied from a variety of sites where *Toxicodendron diversilobum* and the various poison-ivies grew, most of the common and widespread taxa occupy such a variety of habitats that the samples tell us little. The profiles which were examined demonstrate only a segment of the range of soil types in which these taxa grow: *T. rydbergii*, *T. diversilobum*, *T. radicans* subsp. *radicans*, *T. radicans* subsp. *negundo*, and *T. radicans* subsp. *pubens*. Even digging of soil pits would not be necessary to indicate that these plants will grow in a wide range of soils. They seem to be absent from podzols and heavily leached lateritic soils, however, and only rarely make incursions into peat. One taxon which seems to show narrow ranges of soil preference is *Toxicodendron toxicarium*; hence, this plant's soil requirements were examined more extensively.

Soil samples are of particular value from regions wherein several taxa form putative hybrids. If the parent taxa generally inhabit different kinds of soils, then a sample of the soil in which a suspected intermediate is growing may be used to complement morphological data to confirm the hybrid nature of the population. That is to say that the probability that the individual is a hybrid is increased if the individual appears to be growing in a soil that is also intermediate between the extremes preferred by its possible parents. Such samples have been used in corroborating the hybrid nature of populations of *Toxicodendron toxicarium* and *T. radicans* subsp. *radicans*, as will be shown later.

As one may note from collection record data, *Toxicodendron diversilobum, T. rydbergii,* and several subspecies of *T. radicans* generally grow well — and, in fact, reach optimum growth conditions — on floodplains. In those regions where the soils have been sampled also, individuals were climbing nearly every tree and formed a ground cover approaching 100% in the undifferentiated river alluvium. Such soils were determined to be an Underwood stony loam near Hood River, Oregon where *T. diversilobum* and the hybrid between it and *T. rydbergii* grew. The floodplain soil was a Genessee silt loam in East Lansing and Saginaw, Michigan, where *T. radicans* subsp. *negundo* was abundant.

The soil preferences for *Toxicodendron radicans* subsp. *negundo* were examined in a small study within Baker Woodlot on the Michigan State University campus for which a detailed soil map was available. The populations of poison-ivy were mapped for correlation with the soil patterns. To be sure, soils could not be adjudged to be the only factor operating to determine distribution patterns of the plant, but the conditions suggest that they are involved to a large measure.

Baker Woodlot (Ingham Co., East Lansing, Michigan. T. 4N., R. 1W., SW 1/4 Sec. 19) is probably a fragment of the forest that was cut over about one hundred years ago inasmuch as the oldest trees are about a century old. It is predominantly a beech-maple woods, but there are pockets of other tree assemblages that appear to be related to soil substrate and soil moisture. *Toxicodendron radicans* subsp. *negundo* was expected to be common at the edge of the woods where light conditions would be more suitable than those inside the dense canopy, but it will be seen that some factor other than light must be involved in producing somewhat contrary data.

The "edge effect" is manifest on the east side of the woodlot where poison-ivy is found commonly. The soils in which the plant is growing have a medium to high natural fertility and moderate to high available moisture. On the south side of the woods there is little poison-ivy despite an improved light regime from that inside the woods. The south side is clearly disturbed. It serves as a railroad right-of-way, was clear-cut long ago and planted with pine and locust. For the most part, the soils which occur on the south side are — with the exception of Miami loam, one of the better agricultural soils of the state — poorly drained with low natural fertility and with low or variable moisture available for uptake. Such soils are Coloma loamy sand, Hillsdale sandy loam, Locke sandy loam, Berrien sandy loam, Granby loamy sand, Carlisle muck, and the Washtenaw soil. Poison-ivy is likewise uncommon along the west and north edges of the woods. In the northwest corner is a patch of Spinks loamy fine sand which supports a tangle of brambles, gooseberries, and trees, but no poison-ivy. The area is lower than much of the woods and supports a vegetation that is fairly open to light. Presumably it is the low fertility which has precluded its supporting any population of poison-ivy.

Perhaps this analysis of a single woods, its soils, and its poison-ivy population can form a generalization about *Toxicodendron radicans* subsp. *negundo* and its soil requirements. Contrary to popular opinion, poison-ivy is not ubiquitous, but rather requires fairly rich soils. It is all but missing from soils which are low in fertility, or in available moisture, and does not generally grow in standing water. Whereas the plant generally was found to be uncommon on the poorly drained Wauseon soil (composed of a two-storied parent material: a fine sandy loam to loamy fine sand on top of a clay loam to silty clay loam till lower story), it was abundant on this soil surrounding a muck patch in the northern center of the woods. This abundance is presumably attributable to edge effect (border of an open *Cephalanthus* community), to increased fertility, and to the greater drainage afforded by the increase in slope. Poison-ivy thus appears to grow best in soils of high nutrient value and good, but not excessive, drainage.

From the soils sampled for *Toxicodendron rydbergii* populations, it appears that this species generally inhabits slightly more alkaline soils than does *T. radicans* subsp. *negundo. Toxicodendron radicans* subsp. *radicans*, from similar types of soils studies, appears to inhabit slightly more acid soils than either of the taxa mentioned above. Both of these generalizations are admittedly oversimplifications, especially in view of the fact that only six profiles were examined for *T. rydbergii* and five for *T. radicans* subsp. *radicans.*

When one considers the broad geographical sources of these soil samples (New England to the Pacific Northwest and to Florida), the data assume a greater significance despite their apparent skimpiness. In examining the soil profiles for those sites in which *Toxicodendron radicans* subsp. or *T. diversilobum* were found, the A horizons of the soil — and to a lesser extent, the upper B — seem to be the most significant in determining growth conditions for the plant, for it is in the A where maximum root development takes place. Only occasionally do roots penetrate to the B horizon, and then only in the upper B. It is perhaps for this reason that *T. radicans* is virtually absent from well-developed podzols or laterites wherein the A horizon is highly leached of minerals, especially Ca and Mg.

A study was made to determine the mineral nutrient requirements for poison-ivy. Seeds of various taxa were germinated on filiter paper in petri dishes and then transferred to a series of hydroponic solutions. Seedlings were grown in complete nutrient solution as a control, and in a series of solutions lacking respectively Ca, Mg, P, K, Fe, N, and S. Four replicates, involving different taxa each, were carried out in the greenhouse. After two months, the experiment was concluded and evaluated.

Seedlings grown in complete nutrient solutions progressed well. Those grown in Mg-poor solutions initially performed poorly and dropped all leaves, but axillary buds developed and the plants were relatively healthy at the end. Furthermore, plants grown without Mg developed the longest roots. Except for Ca, no one mineral nutrient seemed entirely crucial. Absence of Fe produced mottling on the leaves and some chlorosis; absence of NO_3 resulted in chlorosis, etc. In Ca-poor solutions, however, the most marked effect of all resulted. The seedlings did not develop beyond the cotyledon stage before they died. Even though no tests were run to determine at what minimal concentration calcium becomes critical, it appears safe to say that calcium is the most important of the elements tested in the soil for the growth of taxa in the poison-ivy complex.

It was noted earlier that *Toxicodendron rydbergii* has generally been found growing in soils with fairly high concentrations of calcium. In agricultural sites, these soils would be described as not requiring additional lime to support good growth of most common crops. *Toxicodendron diversilobum* has been found in soils with similar Ca concentrations — none analyzed yielded less than 230 ppm of Ca. For *T. radicans* subsp. *verrucosum*, only one soil was found in which the significant concentrations of calcium were below 350 ppm in those horizons in which roots were found. At this site (Harrison County, Texas, east of Marshall), soil calcium in the A and B horizons ranged from 98-231 ppm. Here, poison-ivy was rare, found only with difficulty after a long search, probably because it was at the lower limit of its calcium requirement. Furthermore, *T. radicans* subsp. *verrucosum* has its main distribution on the limestone and dolomite Edwards Plateau and Arbuckle Mountains, where soils are naturally high in calcium.

Only once was *Toxicodendron radicans* subsp. *eximium* studied in the field, in the Chisos Mountains of the Big Bend region of Texas. It was growing in a lithosol on basalt. The calcium content of the soil was determined to be 1099 ppm. The soil in which one population of *T. radicans* subsp. *barkleyi* grew at the edge of an orchard in Galeana, Nuevo Léon, Mexico, was sampled and examined critically in the laboratory. Here the soil calcium was higher than that for any other soil studied, namely, up to 5700 ppm.

For *Toxicodendron toxicarium,* the soil regime is very different. Unlike any other taxon in this complex, it grows in podzols at its northern limit (Lakewood sands in southern New Jersey), but otherwise is mostly confined to well-developed lateritic soils of the red-yellow podzolic great soil groups, both types of soil having a strongly leached A horizon and a well-developed layer of illuviation in the B. The soils are chiefly light textured, at least in the A and B horizons, where maximum root development takes place. They are moderately to strongly acidic, and uniformly have very low concentrations of Ca. Of the nine soil samples from *T. toxicarium* habitats, sampled from seven states throughout the range of the plant, the highest calcium content was found in the B_1 of a loamy sand in Bastrop State Park, Texas (91 ppm) (Fig. 61). The parent material of this soil contained far higher Ca concentrations, but was out of reach of normal root development. Interestingly, there was no *T. radicans* found there. Most soils which were tested in which *T. toxicarium* grew had far lower Ca, even down to 9 ppm. To some extent, K concentrations were also impoverished.

All of the soils in which *Toxicodendron toxicarium* is indigenous have developed under acid-forming litter, thus leading to heavy leaching. Scrub oaks are dominant with pine a usual constituent in this kind of woods except in the western end of the range of *T. toxicarium.* Drainage of the soil is high to excessive. Such soils are the Lakewood sand, a podzol, and the Lakeland sand, Norfolk sand, and Stephenville fine sandy loams, lateritic soils. The differences in these soils are in parent material, extent of horizon development, and thickness of sand over heavier sediments. The Lakeland, Lakewood, and Norfolk sands have

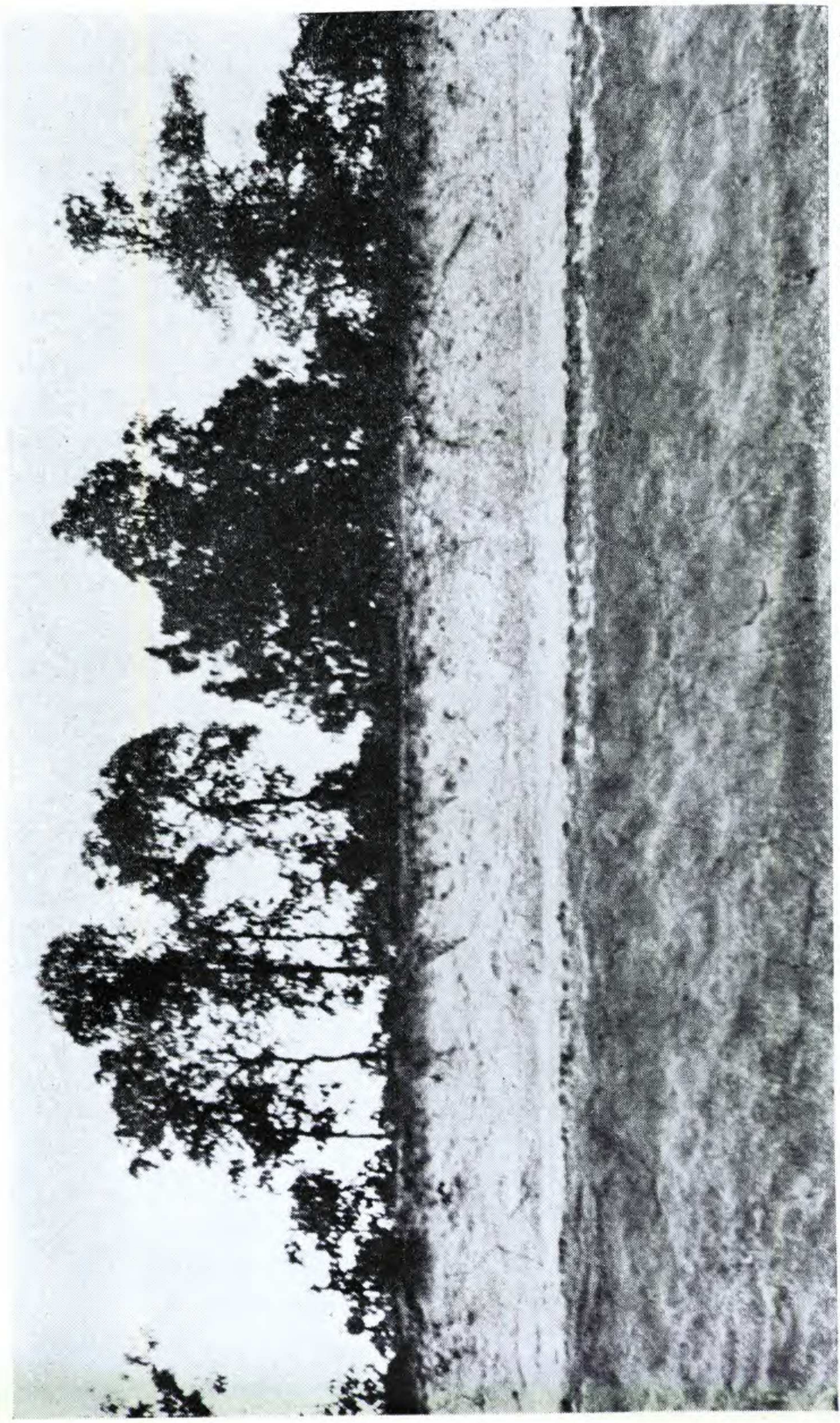

Fig. 61. Road cut in Bastrop County, Texas showing profile of soil in which *Toxicodendron toxicarium* is abundant.

developed on unconsolidated acid sands of the Coastal Plain; the Stephenville series has developed over parent materials derived from reddish sandstone or interbedded sandstone and sandy shale. The latter was the one soil sampled for a poison-oak habitat that was off the Atlantic or Gulf Coastal Plains (in Oklahoma).

The Lakeland soils show little profile development, chiefly because of the low clay content of the parent material, lacking the finer textured subsoils of the Norfolk and Lakewood series. The Norfolk, Lakeland, and Lakewood series differ in that there is a greater thickness of sand over heavier sediments in the Lakewood and Lakeland than in the Norfolk. There are generally heavier textured upper soil horizons in the Norfolk than in either other series. Suffice it to say that all of these soil series have much in common, despite minor differences in profile development. The physical and chemical attributes of the root environment are appreciably similar. No collections were made from any soils determined to be the Orangeburg, a major soil of the Carolina sandhills according to Duke (1961).

Although poison-ivy (*Toxicodendron radicans subspp.*) may inhabit sand dunes and the coastal plain sands, it is not indigenous to the poor soils of the sand scrub as is Eastern poison-oak (*T. toxicarium*). *Toxicodendron radicans* appears to grow in soils that have a higher Ca and usually higher Mg content than the ones in which *T. toxicarium* grows. Furthermore, *T. radicans* generally grows in heavier textured soils than *T. toxicarium*, with less leaching in the A horizon.

Several areas of transition between soil types and corresponding vegetation have been studied where both *Toxicodendron radicans* subsp. *radicans* and *T. toxicarium* were growing intermixed. One area is a gradient along a 5% slope between a Norfolk loamy sand (thin solum phase) and a shallow, incipient Lakeland sand north of Columbia, South Carolina. There is abundant poison-ivy at the lower end of the slope in a heavy-textured soil, poison-oak at the upper end in a shallow coarse sand, and both in the middle of the zone described in greater detail in the section of this paper on Community Specificity for *T. toxicarium* (Fig. 62). A second plot that was studied is in an extensive area of essentially transitional zone between a mesic hammock community and a sandhills community in the San Felasco region of Alachua County, Florida. A third area where poison-ivy was found in association with Eastern poison-oak was in an oak-pine woods in Lincoln County, Mississippi (T. 7N., R. 7E.).

The soil in the South Carolina site where poison-ivy and poison-oak both occur lies between a sandy clay and loamy coarse sand and has been determined to be a sandy loam. The lower (poison-ivy) end of the gradient has finer textured soil than the upper (poison-oak) end and a higher Ca content than either the middle or upper end (44 ppm vs. 21 ppm in the middle vs. 16 ppm in the top for the A_1). The pH is slightly higher in the middle of the gradient than at either end. As the finer particles become less prevalent, the soil becomes more conducive to the growth of poison-oak and less to that of poison-ivy. The same is true as the calcium content drops, especially in the root zone of the A and upper B horizons (see Tables 24 and 25, and Fig. 62).

The Florida site is mapped in the Lakeland series (being only a few miles from the type location where the series was established) as a sandy loam. The texture is finer than that of the adjacent woods where only poison-oak grows, the soil of which is mapped as a Lakeland sand. The pH in the transition zone is higher and has a higher Ca content in the upper soil horizons than in the Lakeland sand which supports poison-oak but no poison-ivy.

The Mississippi site was determined to be on a Bude silt loam, poorly drained, low in fertility, and slightly eroded (Milbrandt, *et al.*, 1963). Its Ca content was moderate — 273 ppm — at the lower end of the presumed tolerance range for *Toxicodendron radicans* subsp. *radicans*, but higher than that recorded for most poison-oak sites. This soil may be looked upon as an intermediate habitat between the usual soil types in which either poison-ivy or poison-oak are normally found, but within the tolerance ranges of both. Although poison-ivy will usually live in the range of particle

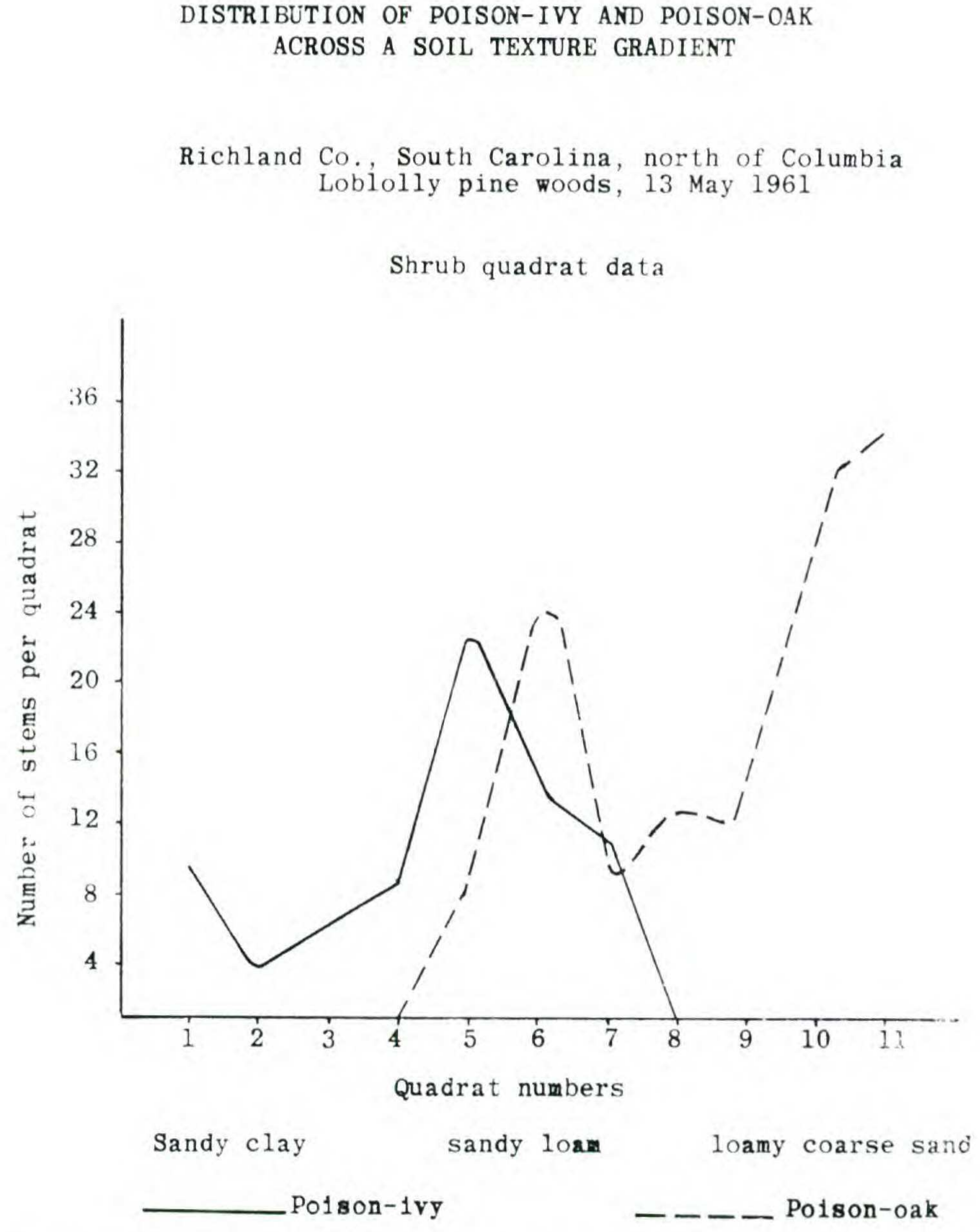

Fig. 62. Distribution of Poison-ivy (*Toxicodendron radicans* subsp. *radicans*) and Eastern Poison-oak (*T. toxicarium*) across a soil texture gradient. Quadrat numbers are the average of two sub-quadrats each, measured along a line 110 m. long and sampled at 10 m. intervals.

size included in a silt loam, the low fertility of this profile makes it a marginal site for poison-ivy.

In summary, one may conclude that *Toxicodendron radicans* subsp. *radicans* inhabits soils which are higher in pH,

TABLE 24. SOIL PROFILE ANALYSIS OF OAK-PINE WOODS, COLUMBIA, SOUTH CAROLINA

Zone	Taxon	Gillis Collection Number	Horizon	Horizon Texture	pH	Ca	Mg	P	K
1	*T. radicans*	*4016*	A_1	sandy clay	4.47	44.5	8	2.4	8
			A_2	sandy clay	5.09	113.5	6	1	5.6
			B_1	sandy clay	4.68	35	5	1.6	6.4
			band in B_1	sandy clay	4.86	63	4	0.5	4.5
			B_2	loamy sand	4.73	15	0	1.0	4
			C	sand	4.38	113	20	1.1	12.4
2	*T. radicans*	*4569*							
	T. toxicarium	*4017*	A_0	sandy loam	5.82	11	0	1.1	3
			A_1	sandy loam	4.83	21	4	1.6	3
			A_2	sandy loam	5.52	15	8	1.5	8.5
			B_1	sandy loam	5.14	15	4	0.9	6
			B_2	sandy loam	5.57	10	6	9.6	2
			C	sand	6.51	85	12	15.8	12.5
3	*T. toxicarium*	*4600*	1	loamy sand	4.53	38	6	1.3	8.5
			2	loamy sand	4.33	16	2	1.7	2
			3	loamy sand	4.99	22	3	1.4	6
			4	sand	4.80	12	2	1.4	4.4

TABLE 25. SOIL PROFILE CHARACTERISTICS OF AREAS WHERE BOTH *T. RADICANS* AND *T. TOXICARIUM* GROW

Locality	Taxon	Gillis Collection Number	Soil Type	Horizon	Horizon Texture	pH	Ca	Mg	P	K
Mississippi	*T. radicans*	*5980*	Bude silt loam	A	loam	6.2	273	6.8	0.5	10.5
	T. toxicarium	*5979*								
S. Carolina	*T. radicans*	*4569*	Lakeland loamy sand	A_0	sandy loam	5.82	11	0	1.1	3
	T. toxicarium	*4017*		A_1	sandy loam	4.83	21	4	1.6	6.4
				A_2	sandy loam	5.52	15	8	1.5	8.5
				B_1	sandy loam	5.14	15	4	0.9	6

				B_2	sandy loam	5.57	10	6	9.6	2
				C	sand	6.51	85	12	15.8	12.5
Florida	*T. radicans* *T. toxicarium*	*4345*	Lakeland sandy loam	A_1	sandy loam	5.00	32	10	3	4.5
				A_2	sandy loam	5.25	28	12	2	4.5
				B	sandy loam	5.58	80	24	2.5	4.5
				C	sand	6.44	715	8	2	4.5

higher in nutrient concentrations (especially calcium and magnesium), and heavier textured than those in which *T. toxicarium* will grow. There is no clear-cut break between the requirements of one and the other, at least from the data presented herein, but rather an overlap of habitat requirements leading to the occasional ecotone wherein both species may be found intermixed. These ecotones are characterized by an intermediate type of soil, accompanied by an intermediate type of vegetation between a mesic woods and a sandhills vegetation — a woodland savanna.

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